Statistical Studies on Cowrie Radulae

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(2 Textfigures)

In these last two years, Mr. R. S. Benton and Mr. W. O. Cernohorsky have sent us several thousand cowries from various localities of Kenya and Fiji, respectively. All these shells contained the complete animals, dried or still soft by being packed in cotton wool wet by spirits, so that we could ascertain the sex of each animal by presence or absence of a penis, and preserve the radula mostly in its entire length.

This rich material seems to be suitable to elucidate the correlation between the following characters:

- L The length of the shell, measured by a vernier caliper in tenths of a millimeter.
- ♀ Female sex of the animal.
- ♂ Male sex of the animal.
- r The number of rows composing the complete radula, the terminal "nascentes" included.
- m The maximum breadth of the median tooth of the radula, expressed in thousandths of a millimeter: the figures represent the mean of five medians measured in each specimen.
- dr The total length of the radula, expressed in tenths of a millimeter; it has been calculated by multiplying the number of rows (r) by the average distance (d) between the basal edges of two adjacent medians; d has been stated by measuring the length of the area occupied by 30 to 40 rows in various parts of the radula, in thousandths of a millimeter.

The mathematical significance of differences (Schilder, 1961b) has been marked as follows:

°	$P > 0.01$	No difference
*	$P < 0.01$	Difference certain
**	$P < 0.001$	Difference strictly proved

HISTORICAL REVIEW

In previous papers we have shown, though by far scantier material, the following relations among specimens of the same species:

1. The average L of ♂ is mostly smaller than that of ♀ (Schilder, 1962b).
2. r does not depend on L, whereas m and dr are correlated to L (Schilder, 1960).

Therefore, we have been enabled to establish the following indices:

r/12 = r:12 = number of rows, expressed in dozens (10 = 114 to 126 rows).
m/L = 2000 m:L = relative breadth of the median.
dr/L = 100 dr:6L = relative length of the radula.

The constants mentioned in these formulae have been chosen so that the average index of all cowries becomes 10 in every character; therefore, indices exceeding 10 indicate relatively numerous rows, broad medians, and long radulae, while indices smaller than 10 indicate less numerous rows, narrower medians, and shorter radulae than would be expected from the sum of all cowry species (Schilder, 1960).

We have shown that in Monetaria r/12 of ♀ is larger than that of ♂, while m/L of ♀ is smaller than that of ♂ (Schilder, 1961S), and dr/L is rather similar in both sexes (Schilder, 1962a): the females have more numerous rows than the males, but smaller teeth, so that the length of the radula ribbon becomes nearly equal.

The figures indicating the average indices are often quite similar in allied species, while they distinctly differ in species placed in different genera or even subfamilies conchologically (Schilder, 1941), so that they may confirm or correct the taxonomy (Schilder, 1960, 1961c, 1962b).

RECENT RESEARCH

The present paper is an attempt to confirm or to emend these former results by extending the investigations to larger series of specimens of still more species.

The correlation between the length of the shell (L), and the number of rows of the radula (r), the breadth of its median (m), and the length of the ribbon (dr) may be shown once more by 66 male specimens of Lyncina lynx Linnaeus, 1758, collected by R. S. Benton within an area of about 63 meters at Shimoni on the southern border of Kenya, from March 1961 to April 1962. In Fig. 1, r indicates the number of rows, L and dr have been expressed in millimeters, m in hundredths of a millimeter; the results clearly are similar to those observed in Monetaria, mentioned above.

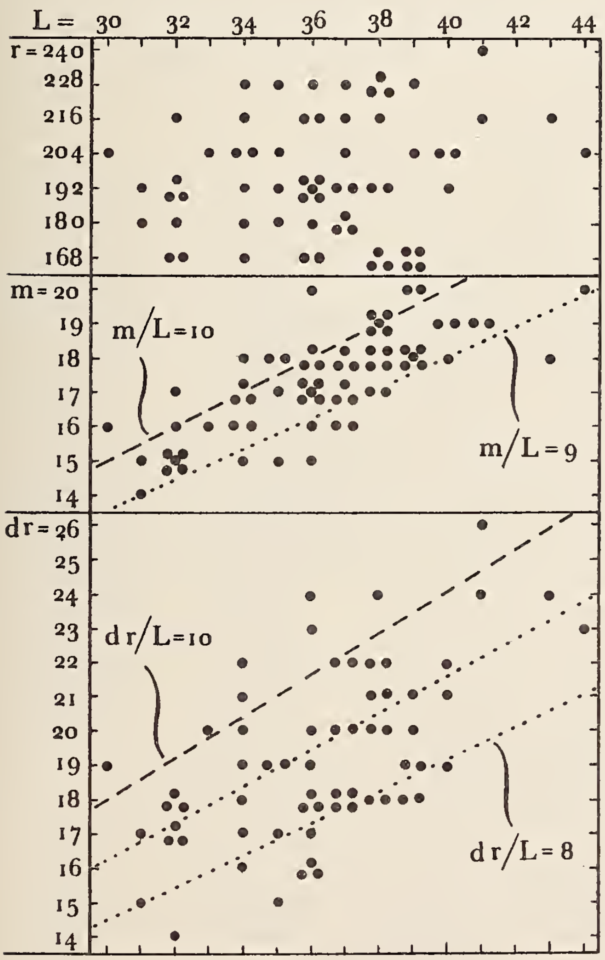

Figure 1: See Text for Explanation

The correlation between L and m may also be illustrated by Fig. 2, which shows the mean of 15 species examined in large numbers. The letters indicate the means of females, the arrow-heads those of males:

a = Luria isabella Linnaeus, 1758
b = Mauritia eglantina Duclos, 1833
c = Lyncina lynx Linnaeus, 1758
d = L. vitellus Linnaeus, 1758
e = L. carneola Linnaeus, 1758
f = L. titan spec. nov.
g = Monetaria annulus Linnaeus, 1758
h = M. moneta Linnaeus, 1758
i = Erosaria helvola Linnaeus, 1758
k = E. erosa Linnaeus, 1758
l = E. lamarckii Gray, 1825
m = Erronea errones Linnaeus, 1758
n = E. caurica Linnaeus, 1758
o = Palmadusta fimbriata Gmelin, 1791
p = Bistolida teres Gmelin, 1791

These means are distinctly arranged along the line - - - - - - - indicating the index m/L = 10, but Luria isabella exhibits an exceptionally large median. The arrows seem to point in various directions, but they show that the shells (L) of males are smaller than or equal to those of females, but never larger, whereas the relative size of medians of males mostly exceeds those of females, though there may be sometimes no difference (as in Lyncina carneola) or even an exceeding of males by females (L. isabella,, L. vitellus).

As all cowry species examined hitherto exhibit such a distinct correlation between L, m, and dr, but evidently the independence of r (Schilder, 1960; 1961a, c; and Fig. 1), the use of the indices explained above seems to be justified; therefore, we shall restrict our further research to these indices only.

The range of variation of the indices r/12, m/L, and dr/L may be illustrated by Table 1: it contains the variation of the specimens of each sex in several selected species. The significance of the differences between the means of ♀ and ♂ has been indicated by asterisks as explained above. The average deviation (Σ) of all species enumerated in Table 2 is in r/12 = 1.23, m/L = 1.29, dr/L = 1.45, varying from 0.8 to 2.7, 0.5 to 2.3, and 0.6 to 2.7, respectively.

Table 2 indicates the mean indices r/12, m/L, and dr/L in each sex of 15 frequent species (represented in Fig. 2). These indices, which have been reduced to one decimal, are preceded by the number of examined specimens (in parentheses). In each index, the columns

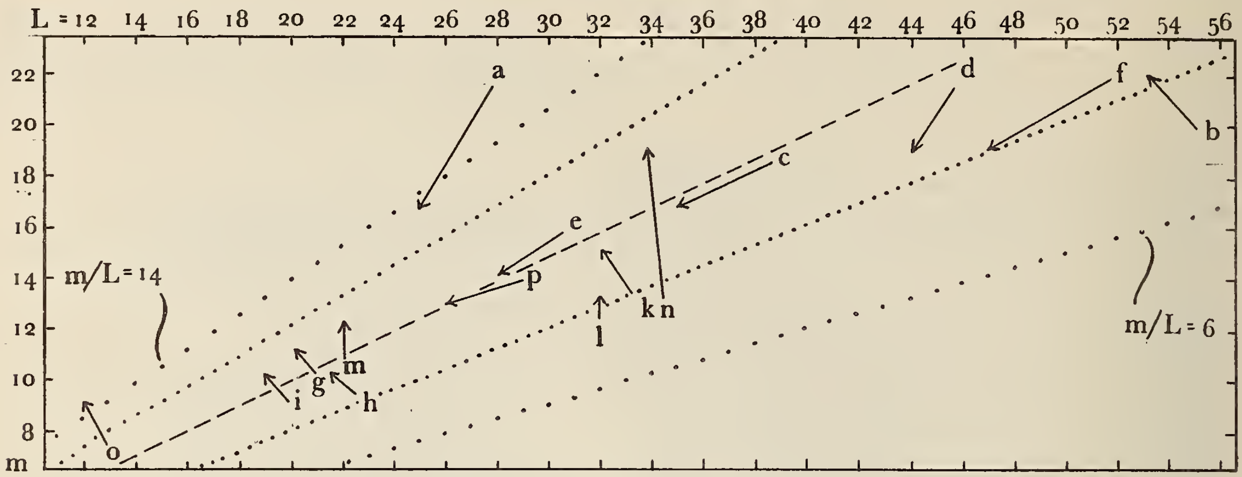

Figure 2: See Text for Explanation

Table 1

Range of Variation of Three Indices in Some Cowrie Species

Species	Sex	4	5	6	7	8	9	10	11	12	13	14	15	Mean Difference
		Index												
Number of Rows ($r/12$)														
Luria isabella	♀	—	—	—	—	4	7	13	16	11	5	1	2	10.88)**
	♂	—	—	—	3	13	10	21	8	9	1	1	2	9.97
Monetaria annulus	♀	—	—	—	1	2	6	21	20	22	5	2	—	10.94)**
	♂	—	—	—	—	6	25	13	4	3	—	—	—	9.47
Erosaria erosa	♀	—	—	—	—	6	13	22	17	5	2	—	—	10.12)**
	♂	—	—	—	—	9	21	25	10	—	—	—	—	9.55
Relative Breadth of Median (m/L)														
Mauritia eglantina	♀	—	—	7	27	12	3	—	—	—	—	—	—	7.22)**
	♂	1	2	2	9	16	12	4	—	—	—	—	—	7.93
Erronea caurica	♀	—	1	1	13	38	8	1	1	1	—	—	—	7.98)**
	♂	—	—	—	1	4	6	6	8	8	7	6	2	11.29
Lyncina carneola	♀	—	—	—	2	3	5	41	46	12	9	1	—	10.71)**
	♂	—	—	—	—	—	20	53	29	5	3	—	—	10.25
Lyncina titan	♀	—	—	—	2	29	23	7	—	—	—	—	—	8.57)**
	♂	—	—	—	11	42	13	4	—	—	—	—	—	8.14
Lyncina lynx	♀	—	—	—	—	1	33	43	18	5	—	—	—	9.93)°
(Kenya)	♂	—	—	—	—	—	39	37	17	3	—	—	—	9.83
id.	♀	—	—	—	—	7	13	6	—	—	—	—	—	8.96)°
(Fiji)	♂	—	—	—	—	2	14	3	—	—	—	—	—	9.06
Relative Length of the Radula (dr/L)														
Lyncina vitellus	♀	—	—	—	—	1	6	12	6	3	1	—	—	10.24)°
	♂	—	—	—	—	—	7	8	7	3	1	—	—	10.35
Erosaria helvola	♀	—	—	1	2	9	24	24	9	5	1	—	—	9.60)°
	♂	—	—	1	1	4	15	14	12	5	1	—	—	9.91
Erosaria lamarckii	♀	1	2	2	4	7	6	1	—	—	—	—	—	7.57)*
	♂	—	—	2	3	7	8	6	2	—	—	—	—	8.68
Erronea errones	♀	1	—	3	9	4	1	2	—	—	—	—	—	7.30)**
	♂	—	—	—	2	2	4	—	2	2	—	—	—	9.33

(see text for explanation)

for females and males are separated by the sign of the sex in which the index is larger and by the degree of significance of the difference between the sexes (see above). At the bottom, we have added three species, the numerous specimens of which came from two different regions: in each, the third line indicates the significance of local or racial differences in each sex (in each column the respective index is larger in the named region, with the indicated significance).

The East African and the Pacific specimens of Lyncina lynx and Monetaria moneta significantly differ in m/L and dr/L of both sexes, while r/12 is instead identical; in Erosaria erosa, however, such a significant difference exists in r/12 of males only. Besides, we see from Table 2 that in several species the sexes differ most significantly in all indices of the radula (Luria isabella, M. annulus, M. moneta, E. erosa, and Erronea caurica), while other species differ in one index or in the other, or even in none (L. lynx and Bistolida teres); the significance of sexual differences in the radula seems to be scattered as a specific character only, as hardly any relation to the affinity of species can be observed. On the other hand, the magnitude of the indices seems to be rather similar in many allied species, as well as the sex exhibiting the larger indices even if their differences cannot be proved as mathematically significant.

This fact may be reinforced by Table 3, which contains 50 species arranged according to Schilder (1941).

The three figures indicate the mean indices r/12, m/L, and dr/L, calculated from all examined specimens including those whose sex is unknown. The added signs ♀ or ♂ indicate the sex in which the index is larger, with **, *, or ° designating the degree of significance of the sexual difference. The absence of these signs points to a scarcity of specimens of known sex, which precludes stating them with satisfactory accuracy.

Table 2

Mean Indices for Both Sexes in Fifteen Species of Cowries

Species	Area	♀ r/12		♂	♀ m/L		♂	♀ dr/L		♂
Luria isabella	Indopacific	(59) 10.9	♀**	(68) 10.0	(62) 15.2	♀**	(71) 13.7	(59) 14.1	♀**	(68) 12.2
Mauritia eglantina	Fiji	(34) 13.0	♀**	(36) 11.4	(49) 7.2	♂**	(46) 7.9	(34) 10.2	♂°	(36) 10.4
Lyncina lynx	Indopacific	(119) 16.7	♀°	(105) 16.3	(126) 9.7	=°	(113) 9.7	(119) 9.2	♀°	(105) 9.0
Lyncina vitellus	Indopacific	(29) 17.8	♂°	(26) 19.0	(31) 9.7	♀*	(31) 9.0	(29) 10.2	♂°	(26) 10.3
Lyncina carneola	Kenya	(108) 17.8	♂°	(95) 18.0	(119) 10.7	♀**	(110) 10.3	(108) 12.3	♀°	(95) 11.9
Lyncina titan	Kenya	(46) 19.1	♂°	(58) 19.4	(61) 8.6	♀**	(70) 8.1	(46) 10.6	♀°	(58) 10.3
Monetaria annulus	Indopacific	(79) 10.9	♀**	(51) 9.5	(102) 9.7	♂**	(65) 11.4	(78) 9.2	♂**	(52) 10.2
Monetaria moneta	Indopacific	(191) 9.0	♀**	(107) 8.5	(244) 8.2	♂**	(164) 9.6	(191) 7.6	♂**	(107) 8.5
Erosaria helvola	Indopacific	(75) 9.4	♀**	(53) 8.7	(100) 9.3	♂**	(74) 10.2	(75) 9.6	♂°	(53) 9.9
Erosaria erosa	Indopacific	(65) 10.1	♀**	(65) 9.6	(81) 7.4	♂**	(81) 8.8	(65) 7.6	♂**	(65) 8.6
Erosaria lamarckii	Port Reitz	(23) 10.3	♂°	(28) 10.5	(29) 7.2	♂*	(40) 8.0	(23) 7.6	♂*	(28) 8.7
Erronea errones	Pacific	(20) 8.2	♀°	(12) 8.0	(37) 9.5	♂*	(24) 10.8	(20) 7.3	♂**	(12) 9.3
Erronea caurica	Kenya	(44) 9.0	♀**	(38) 8.3	(64) 8.0	♂**	(48) 11.3	(44) 6.8	♂**	(38) 8.8
Palmadusta fimbriata	Kenya	(17) 8.5	♀*	(14) 7.3	(28) 11.4	♂**	(16) 13.4	(17) 7.5	♂*	(14) 9.4
Bistolida teres	Indopacific	(13) 6.8	♂°	(10) 7.3	(18) 10.1	♀°	(18) 9.9	(13) 5.2	♂°	(10) 5.7
Lyncina lynx	Kenya	(94) 16.8	♀*	(89) 16.2	(100) 9.9	♀°	(96) 9.8	(94) 9.4	♀°	(89) 9.1
	Fiji	(25) 16.4	♂°	(16) 16.6	(26) 9.0	♂°	(17) 9.1	(25) 8.2	=°	(16) 8.2
	Kenya : Fiji	Kenya°		Fiji*	Kenya**		Kenya**	Kenya**		Kenya**
Monetaria moneta	Kenya	(158) 9.1	♀**	(86) 8.5	(197) 8.0	♂**	(129) 9.4	(158) 7.3	♂**	(86) 8.2
	Pacific	(33) 8.9	♀°	(21) 8.6	(47) 9.3	♂**	(35) 10.3	(33) 9.0	♂**	(21) 9.9
	Kenya : Pacific	Kenya°		Pacific°	Pacific**		Pacific*	Pacific**		Pacific**
Erosaria erosa	Kenya	(51) 10.1	♀**	(46) 9.3	(61) 7.5	♂**	(56) 9.0	(51) 7.7	♂**	(46) 8.7
	Pacific	(14) 10.4	♀°	(19) 10.1	(20) 7.1	♂**	(25) 8.5	(14) 7.4	♂*	(19) 8.5
	Kenya : Pacific	Pacific°		Pacific**	Kenya*		Kenya°	Kenya°		Kenya°

(see text for explanation)

Table 3

Three Indices for Fifty Species of Cowries

	r/12	m/L	dr/L		r/12	m/L	dr/L
Cypraeinae:				*Staphylaea staphylaea*	8 ♀*	12 ♂*	7 ♂°
Luria isabella	10 ♀**	14 ♀**	13 ♀**	*S. limacina*	7 ♀	15 ♂	8 ♂
L. tessellata	16	10	11	*Nuclearia nucleus*	10	8	7
Mauritia arabica	12 ♀	8 ♀	12 ♀	Cypraeovulinae:			
M. eglantina	12 ♀**	8 ♂**	10 ♂°	*Notocypraea piperita*	7	11	6
M. scurra	14	8	12	*N. bicolor*	6	10	5
M. histrio	11 ♀°	9 ♂°	10 ♂*	*Umbilia hesitata*	8	9	8
M. maculifera	14	8	13	*Erronea xanthodon*	9	10	10
M. mauritiana	16 ♀	7 ♀	10 ♀	*E. errones*	8 ♀°	10 ♂*	8 ♂**
Talparia talpa	16	7	5	*E. cylindrica*	8	10 ♂	8
Cypraea tigris	16 ♂°	8 =°	11 ♂°	*E. caurica*	9 ♀**	10 ♂**	8 ♂**
Lyncina lynx	17 ♀°	10 ♀°	9 ♀°	*E. felina*	9	8	7
L. vitellus	18 ♂°	9 ♀*	10 ♂°	*Palmadusta punctata*	7	10	8
L. carneola	18 ♂°	10 ♀**	12 ♀°	*P. clandestina*	9 ♂	10 ♀	5 ♀
L. titan	19 ♂°	8 ♀**	10 ♀°	*P. artuffeli*	8	11	4
Nariinae:				*P. lentiginosa*	9	9	6
Monetaria annulus	10 ♀**	11 ♂**	10 ♂**	*P. gracilis*	7 ♀°	11 ♂°	7 ♂**
M. moneta	9 ♀**	9 ♂**	8 ♂**	*P. japonica*	6	12	6
Erosaria boivinii	9	10	9	*P. fimbriata*	8 ♀*	12 ♂**	8 ♂*
E. helvola	9 ♀**	10 ♂**	10 ♂°	*Bistolida*			
E. caputserpentis	10	10	9	*quadrimaculata*	9	8	6
E. erosa	10 ♀**	8 ♂**	8 ♂**	*B. teres*	7 ♂°	10 ♀°	5 ♂°
E. nebrites	10	8	9	*B. kieneri*	6 ♂	12 ♀	5 ♀
E. miliaris	11	8	8	*B. hirundo*	6	10	4
E. eburnea	9	7	6	*B. stolida*	7 ♀	10 ♂	4 ♀
E. lamarckii	10 ♂°	8 ♂*	8 ♂*	*Ovatipsa chinensis*	8	13 ♀	8
E. turdus	10	9	9	*Cribraria cribraria*	14	6	7

(see text for explanation)

Table 3 shows the following interesting facts which may be easily recognized by plotting the indices against the taxonomical arrangement of species:

r/12 ranges from 6 to 19: it is large (numerous rows) in A (maximum in Ae), medium in B (small in Bc only), and small in C (except in Cg); the means are 16, 10, and 8.

m/L ranges from 6 to 15: it is smaller (median tooth narrow) in A (but large in Aa) than in B (large in Bc) and in C (small in Cg); the means are 8, 9, and 10.

dr/L ranges from 4 to 13 (the radula is $\frac{1}{3}$ to $\frac{4}{5}$ as long as the shell, index = 8 indicates $\frac{1}{2}$ the shell): it is large (radula ribbon long) in A (except in Ac), medium in B, and small in C; the means are 11, 8, and 6.

Therefore, there is a gradual decrease in r/12 and dr/L from A (the primitive Cypraeinae) over B (Nariinae) to C (the highly developed Cypraeovulinae), so that the radula generally becomes shorter and composed of less numerous rows; on the other hand, the median seems to become gradually larger during the evolution of the family Cypraeidae. There is, however, a great overlapping in the species of these groups, and there are some genera aberrant in some respects, especially Aa, Ac, Bc (while Bd is typical Nariinae), and Cg.

The sexual differences in the indices are far less distinct, as in many groups there are species exhibiting an index larger in females, mixed with those exhibiting the same index smaller in this sex. Generally, the females surpass the males in r/12 only (in 68 percent of r/12, the index in females is larger than in males), while in m/L (43 percent) and dr/L (36 percent) the females less frequently exceed. With regard to r/12, the females exceed chiefly in B and in A (except in Ad and Ae); but in no species of B do the females seem to exceed in m/L nor in dr/L.

Summary

The indices r/12, m/L, and dr/L, indicating the number of rows of the radula, the size of its median, and the length of the radula ribbon (the last two characters related to the length of the shell), seem to represent an accessory argument for the taxonomical arrangement of cowry species and genera.

Acknowledgment

We are very much indebted to Mr. Ronald S. Benton, formerly at Mombasa, Kenya, and to Mr. Walter O. Cernohorsky, at Vatukoula, Fiji, for their admirably unselfish support of our studies by indefatigably collecting large series of cowries at restricted localities, and by preserving them so that the animals can be well examined after being in transit for eight to ten weeks to Germany. Mrs. Edith Kilian, Zoological Institute of the University of Halle, Germany, has carefully prepared several thousand radulae for microscopical research.

ADDITIONAL NOTE

In the present paper we have included also Lyncina titan which we are about to establish in another paper (Archiv für Molluskenkunde, Vol. 91, pp. 4-6, December 1962). Lyncina titan differs from L. carneola (Linnaeus, 1758) chiefly by its enormous size, which is about twice as large and leaves a distinct gap in range of variation between the two sibling species; the limit in size slightly differs in sexes and in populations, but it is always striking. There are also accessory differences, especially in the radula: in L. titan r/12 is larger, but m/L and dr/L are smaller than in L. carneola; all differences are significant in both sexes. We must call L. titan a distinct species, as it lives in some places of East Africa (but not in all places!) together with L. carneola without breeding indeterminable intermediates: it looks like a polyploid species. The East African L. titan must not be confounded with the Polynesian L. leviathan Schilder & Schilder, 1937. The holotype of L. titan has been collected by R. S. Benton in Shimoni (East) at the Southern border of Kenya, 28 August 1961 (coll. Schilder 13208): its formula is 67(57)32:27.

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